

# New data on the taxonomy and distribution of the genus *Littoraria* Griffith and Pidgeon, 1834 (Gastropoda: Littorinidae) in Indo-West Pacific mangrove forests

David G. Reid

Department of Zoology  
The Natural History Museum  
London SW7 5BD, UK  
dgr@nhm.ac.uk

## ABSTRACT

This paper adds new data on mangrove-associated species of *Littoraria* in the Indo-West Pacific region that have accumulated since the taxonomic revision of the group by Reid (1986a). One new species is described from the northeastern Indian Ocean and *L. sinensis* (Philippi, 1847) is distinguished from the similar *L. articulata* (Philippi, 1846) with which it was previously confused. Significant extensions to the distribution ranges of 12 species are reported. The penis, paraspermatozoa and radula of *L. delicatula* (Nevill, 1885) are described for the first time and additional information given on the geographical variation of *L. filosa* (Sowerby, 1832) in Australia. New literature (post-1985) on the entire genus *Littoraria* is briefly reviewed.

## INTRODUCTION

The family Littorinidae is among the most well studied of marine gastropod groups, for it is of worldwide distribution and its members are usually abundant, accessible and easily collected in the intertidal zone (see reviews by McQuaid, 1996a, b). Until some 30 years ago the group was noted for a confused taxonomy based mainly on highly variable shell characters. However, since then the application of techniques of fine anatomy, scanning electron microscopy and molecular biology has resulted in refinement. Within the most well known subfamily, the intertidal and monophyletic Littoriniinae (Reid, 1989a), recent studies recognise 139 species in eight genera: 1 *Melarhaphe* (Rosewater, 1951; Reid, 1989a); 11 *Peasiella* (Reid, 1989b; Reid and Mak, 1998); 2 *Mainwaringia* (Reid, 1986b); 10 *Tectarius* (Rosewater, 1972; Reid and Geller, 1997); 1 *Cenchritis* (Rosewater, 1972; Reid, 1989a); 39 *Littoraria* (Reid, 1986a, 1999a, b, this study); 19 *Littorina* (Reid, 1996) and 56 *Nodilittorina* (Bandel and Kadolsky, 1982; Reid, 1989a, in press a, b). For the subfamily Littoriniinae there is at least a preliminary phylogeny of the genera (Reid, 1989a) and some species-level phylogenies (e.g. Reid et al., 1996; Reid, 1999b), and further molecular phylogenies are

now being produced. For all these 139 species the reproductive mode and habitat are known, and for almost all of them the geographical distribution is recorded in detail. This, therefore, represents a remarkable dataset among marine invertebrates: a relatively well-worked monophyletic group of worldwide (but predominantly tropical) distribution. Once a more robust phylogenetic framework is achieved it should become a model system for the study of macroevolutionary processes (e.g. *Littorina*, Reid et al., 1996). Meanwhile, it is important to understand the systematics of these species accurately and to record their distributions as precisely as possible.

The modern concept of the genus *Littoraria* as a monophyletic group was established by Bandel and Kadolsky (1982) and Reid (1986a, 1989a); before this the species were generally included in *Littorina*, a large polyphyletic assemblage. The genus is almost exclusively tropical in distribution and the highest diversity is found in the Indo-West Pacific biogeographic region. At the species level, the classification of this group underwent a considerable change following a revision by Reid (1986a) of the Indo-Pacific species associated with mangrove habitats. Using a range of evidence from anatomy (in particular of penis, paraspermatozoa and pallial oviduct), radula, shell morphology, habitat, distribution, and copulation frequency, it was shown that 20 species could be discriminated whereas only 3 had been commonly distinguished previously. Since this revision, new collections have accumulated. As a result, some of the earlier conclusions must be revised and three additional species can be recognised in the region. The new material also adds significant extensions to the distributional ranges of some taxa. It is the aim of this paper to describe and redescribe two of the additional taxa (the third will be described elsewhere, Stuckey and Reid, in preparation) and to document some new observations and distributional records. It should be used in conjunction with the earlier work (Reid, 1986a).

At the time of Reid's (1986a) systematic revision, other aspects of the biology of these tropical species had

received relatively little study. However, in the years since then they have received much more attention. Among several remarkable features of *Littoraria* are the association of many species with mangrove trees, leading to studies of their zonation patterns, diet and predation. Some members are ovoviviparous, and many show spawning or feeding migrations with lunar and tidal periodicity. A striking color polymorphism of the shell is shown by species occurring on mangrove foliage and these have emerged as a model system for the study of the maintenance of polymorphism by natural selection. There has also been new work on ultrastructure, egg capsules, radular plasticity, parasitism and genetics. This new literature will be briefly reviewed here.

#### NEW LITERATURE ON *LITTORARIA* SINCE 1985

Reid (1986a, 1989a) listed 36 known species of *Littoraria* worldwide (one of which was unnamed), but detailed descriptions were restricted to those 20 found in association with mangrove trees in the Indo-West Pacific region. Since then the six species occurring in the Eastern Pacific region have been described (Reid, 1999a; see also Reid and Kaiser (2001) for two new records of Indo-West Pacific species in the eastern Pacific) including the unique nonplanktotrophic *L. aberrans* (Philippi, 1846) and the new taxon *L. rosewateri* Reid, 1999. In addition to the single new species described in the present paper, and the recognition of two taxa within '*L. articulata* (Philippi, 1846)' (as used by Reid, 1986a), a further new species from northern Australia is being described elsewhere (Stuckey and Reid, in preparation; see Warmoes et al., 1990, and Reid, 1992a, for additional regional taxonomic accounts). This brings the total for the genus to 39 species.

A preliminary phylogenetic analysis of all *Littoraria* species then known, based on cladistic analysis of morphological characters, was done by Reid (1986a). This has since been revised and updated (Reid, 1999b). The new phylogeny was not well resolved, but supported the monophyly of the subgenera *Palustorina* and *Littorinopsis*, and suggested that the subgenus *Littoraria* was a paraphyletic assemblage; a significant change to the phylogenetic classification of the genus was the combination of five mainly rock-dwelling Indo-Pacific species (*L. pintado* (Wood, 1828), *L. mauritiana* (Lamarck, 1822), *L. glabrata* (Philippi, 1846), *L. coccinea* (Gmelin, 1791), *L. undulata* (Gray, 1839)) in the basal subgenus *Protilittoraria*, which had previously held only *L. pintado* (Reid, 1989a). The fossil record of *Littoraria* is limited, but better than that of other littorinid genera, probably because preservation is more likely in mangrove environments than on high-energy rocky shores. The known fossil species were listed by Reid (1999b) and discussed in the context of vicariant events in the biogeographic history of the clade. A similar history, of Tethyan origin and subsequent vicariance, has been proposed for mangroves by Ellison et al. (1999), who cited the worldwide diversity gradient of *Littoraria* species in support. Extinctions

of marine invertebrates during historical time are rarely reported; *L. flammea* (Philippi, 1847) was included as one of only four possible examples among gastropods discussed by Carlton (1993).

Regrettably little genetic work has yet been undertaken on *Littoraria*. Several studies of allozyme variation within the Australian species have confirmed that the species defined by morphological criteria are indeed distinct (Johnson and Black, 1995; Schmidt, 1995; M. Stuckey, personal communication). Levels of intraspecific genetic variation have been assessed using allozyme markers in *L. angulifera* (Lamarck, 1822) (Janson, 1985) and in the two subspecies of *L. cingulata* (Philippi, 1846) (Johnson and Black, 1995). DNA sequences have so far been published for the 16S ribosomal RNA gene (3 species, Reid et al., 1996) and 18S rRNA gene (1 species, Winnepeemineckx et al., 1995), but have yet to be used for phylogeny reconstruction within the genus. This should be a priority.

Although the genus *Littoraria* is well known as a characteristic inhabitant of mangrove forests, this is not true of all the species. There appears to have been an evolutionary specialisation to the mangrove habitat, since basal species occur exclusively on rocks, or on both rocks and driftwood, whereas only the more derived clades occur on trunks and foliage of mangrove trees (Reid, 1999b). The three-dimensional structure of the mangrove habitat, and frequent sympatric occurrence of several *Littoraria* species, has stimulated numerous accounts of comparative zonation patterns. These have been carried out in Australia and the western Pacific (Cook et al., 1985; Reid, 1985; Boneka, 1994; Catesby and McKillup, 1995), Japan (Ohgaki, 1992), the Caribbean (Gutierrez, 1988) and the eastern Pacific (Blanco et al., 1995; Blanco and Cantera, 1999; Cantera et al., 1999). In general, *Littoraria* species do not seem to be restricted to particular tree species, but are found on characteristic substrates (bark or foliage), at typical tidal heights and in typical horizontal zones (seaward or landward fringes) within the forest; furthermore, the assemblages of species on continental margins and on oceanic islands are different (Reid, 1985, 1986a, 1999a). Some of the typically mangrove-associated species can also be found on sheltered rocky shores, including *L. articulata* (see Crowe, 1997), *L. sinensis* (Philippi, 1847) (accounts of distribution of '*Littorina scabra*' on rocky shores of Hong Kong and southern China probably refer to a mixture of these two species, e.g. Ohgaki, 1985; Yi and Li, 1988; You, 1990) and *L. flava* (King and Broderip, 1832) (Montinho and Alves-Costa, 2000). Ecological data on those species that are found mainly on rocks and driftwood, such as *L. undulata* and *L. coccinea*, are scarce (Poulicek et al., 1994; Sacchi, 1994; Ohgaki, 1995).

Within the mangrove environment those species inhabiting trunks and roots at lower levels on the trees migrate vertically with the tide in order to remain above the water level (Yipp, 1985; Gutierrez, 1988; Ohgaki, 1992; Jensen, 2000). Similar behavior has been reported on rocky shores (Ohgaki, 1993; Svane and Pringgenies,

1997) and displacement experiments have been carried out (Antwi and Ameyan-Akumfi, 1987). In contrast, species typically found at higher levels among the foliage of mangroves are not contacted by the high tide, but become active during rain and heavy dew (Little and Stirling, 1984; Kohlmeier and Behout, 1986; Ohgaki, 1992). *Littoraria irrorata* (Say, 1822) occurs in salt marshes in the southeastern United States, where it climbs the stems of marsh grass and descends to feed on the substrate at low tide. This behavior has been investigated in relation to both thermoregulation (McBride et al., 1989; Williams and Appel, 1989; Henry et al., 1993) and avoidance of predators (Warren, 1985; Vaughn and Fischer, 1988, 1992; Dix and Hamilton, 1993; Duval et al., 1994). This species has been employed in studies of trail following (Stirling and Hamilton, 1986; Tankersley, 1989, 1990; Robbins and Hamilton, 1996). Unlike all other species of the genus, it is entirely temperate in distribution and hibernates during winter (Paul et al., 1989). Aggregation behavior has been described in *L. flava* on rocky shores in Brazil (Montinho and Alves-Costa, 2000).

*Littoraria* species suffer high levels of predation, apparently mainly from aquatic predators, accounting for their avoidance of submersion by the rising tide. In mangrove forests portunid crabs take snails at and below the water surface, while some grapsids are able to climb several metres up into the trees (Maruthamuthu et al., 1985, 1986; Borjesson and Szelistowski, 1989; Reid, 1992b; Boneka et al., 1998). Predatory fish may also be important predators of juvenile *Littoraria* and species from lower vertical levels (Hughes and Jones, 1985; Hughes and Mather, 1986; Borjesson and Szelistowski, 1989; Catesby and McKillup, 1998; Duncan and Szelistowski, 1998). In salt marshes both portunid crabs and predatory gastropods (*Melongena*) attack *L. irrorata* (Warren, 1985; West and Williams, 1986; Dix and Hamilton, 1993; Schindler et al., 1994). There is limited evidence of predation by birds on *Littoraria* species in the mangrove canopy (Reid, 1987; Cook and Garbett, 1992). An unusual predatory association has recently been reported in southern Queensland, where two species of sarcophagid flies are a significant cause of mortality in *L. filosa* (Sowerby, 1832) (McKillup and McKillup, 2000; McKillup et al., 2000; Pape et al., 2000). In Vietnam, South East Asia and India the larger *Littoraria* species are gathered locally for food by humans (Kasinathan and Shanmugam, 1988; Pontiers, 1998).

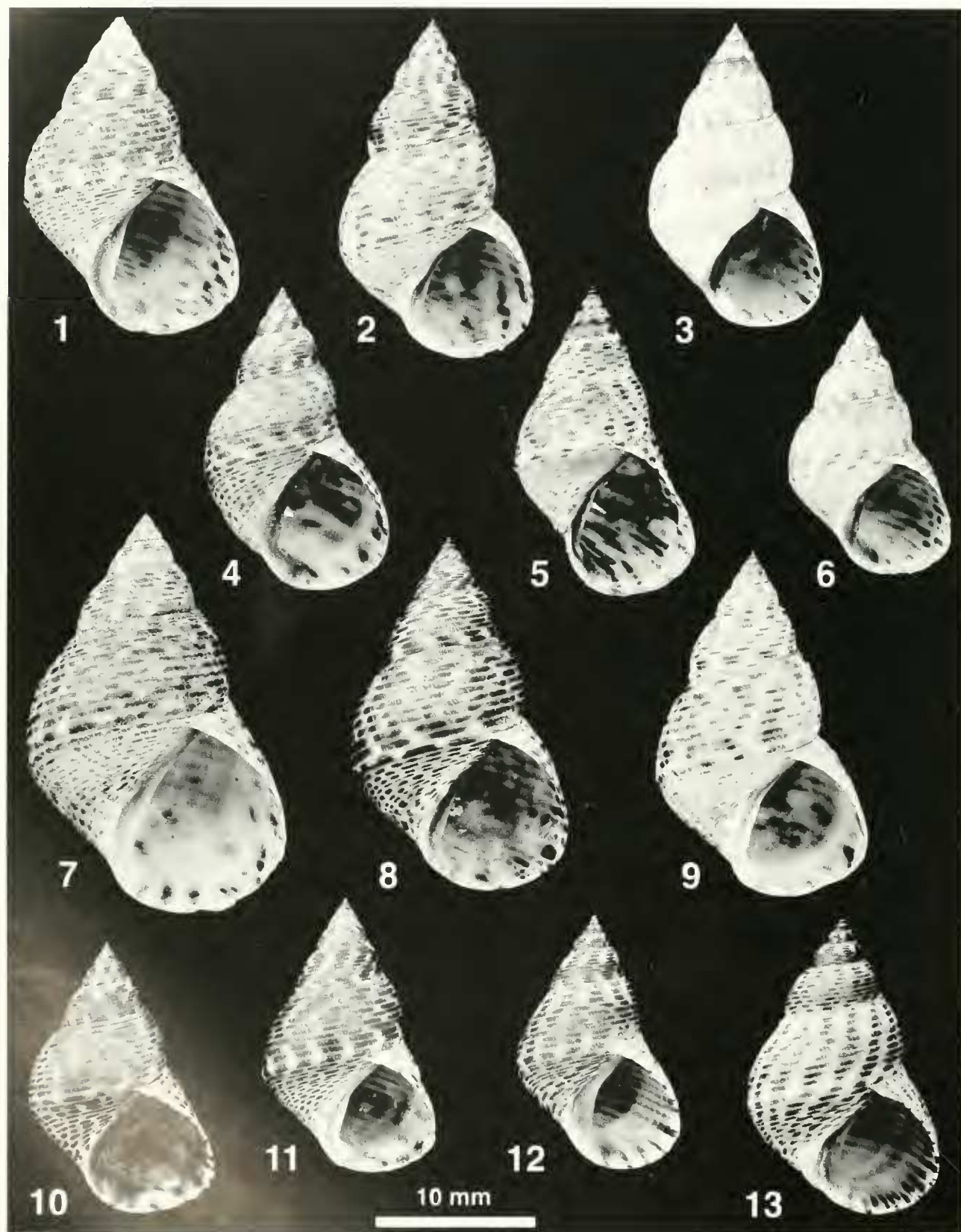
On tropical rocky shores *Littoraria* have been reported to graze on diatoms, microalgae, cyanobacteria and bacteria, but in mangrove and saltmarsh habitats additional sources of food are available. *Littoraria* species appear to be opportunistic grazers, ingesting a range of fungal, algal, detrital and plant material and their role in food webs has been examined (Kemp et al., 1990; Currin et al., 1995). Several investigators have stressed the likely importance of marine fungi in the diet of *Littoraria* inhabiting both mangrove trees (Kohlmeier and Behout, 1986; Christensen, 1998) and grass (Newell and Bär-

locher, 1993; Bärlocher and Newell, 1994a, b; Graca et al., 2000). Whether mangrove plant tissue is a significant food source is debated (Ohgaki, 1990; Jensen, 2000; Lee, 2001) and the composition of the diet may depend upon vertical zonation and tree species (Jensen, 2000). The mechanical function of the radula has not been studied, but it has been shown that the form of the radular teeth differs consistently in specimens of the same species sampled from rock and wood substrates, implying that tooth shape is phenotypically plastic (Reid and Mak, 1999). Growth rates can be rapid in tropical *Littoraria* species, most reaching asymptotic size in six months to one year (Maruthamuthu and Kasinathan, 1985; Burgett et al., 1987; Cruz, 1989; Boneka et al., 1997; Jensen et al., 1999; Jensen, 2000). Breeding and population characteristics have been reported in several *Littoraria* species (Berry, 1986; Maruthamuthu and Kasinathan, 1986; Yi and Li, 1988; Herjanto and Thomas, 1995; Jensen et al., 1999).

The intraspecific variability of littorinid shells has been a common cause of taxonomic confusion in the past. In a morphometric study of *L. angulifera* throughout its Atlantic range, Merkt and Ellison (1998) reported strong intraspecific variation in shell shape, but argued that this was a consequence of ecophenotypic effects rather than genetic differentiation. However, an earlier study of the same species over a more restricted area had reached the opposite conclusion (Janson, 1985). When considering variation between species, it has often been observed that shell thickness decreases in species zoned at higher levels on the trees, reflecting adaptation to the severity of aquatic predation at lower levels (Cook et al., 1985; Borjesson and Szelistowski, 1989; Duncan and Szelistowski, 1998) and the danger of dislodgement in the canopy (McMahon, 1985).

In many *Littoraria* species the most striking aspect of shell variability is the color polymorphism of the shell. Indeed this feature has stimulated the most active field research on the genus, so that species of *Littoraria* have become recognised as a model system for the study of visible genetic polymorphism (Cook, 1992). Unfortunately, early studies suffered from the confusion of several different sympatric species (Hughes and Jones, 1985; Hughes and Mather, 1986). It has been observed that there is a consistent correlation between monomorphic (although still variable) shells and a low-level habitat on trunks and branches, whereas species inhabiting foliage are polymorphic (Cook, 1983, 1986b), although under exceptional circumstances polymorphism has also been reported in a trunk-dwelling species (Cook and Bridle, 1995). The three principal morphs are yellow, brown and pink (or 'orange') and each appears to be cryptic against different parts of the visually varied background of the mangrove canopy, or to mimic elements of the foliage (Cook, 1983; Reid, 1987). Assuming that the polymorphism is genetic in origin and not selectively neutral, there are a number of mechanisms by which it could be maintained by natural selection (Reid, 1987; Cook and Garbett, 1992). Evidence has accumulated for







significant changes in morph frequencies according to the composition of the background (e.g. tree species and abundance of foliage; Reid, 1987; Cook and Garbett, 1989; Cook, 1990a; Schmidt, 1998) and there has been one manipulative field experiment that suggested the operation of frequency-dependent (apostatic) selection (Reid, 1987). Nevertheless, the identity of possible visual predators is a matter of speculation: birds, crabs and even flies have been suggested (Reid, 1987; Cook and Garbett, 1992; McKillup et al., 2000). The differences in thermal properties of the morphs may result in behavioral differences that contribute to site selection and background matching (Cook, 1986b; Cook and Freeman, 1986; Reid, 1987). The color morphs of *L. pallescens* have also been shown to differ in shell strength, size, variance and growth rate (Cook et al., 1985; Cook, 1990b; Cook and Kenyon, 1993; Boneka, 1996; Boneka et al., 1997).

Relatively few new anatomical studies have been carried out since 1986. Egg capsule shape has been documented in a number of additional species (Berry, 1986; Ho, 1987; Mak, 1995). The flagellum-like structure of the paraspermatozoa is a character of phylogenetic significance (Reid, 1999b); this has been named the pseudotrich and has been the subject of structural and ontogenetic study (Healy and Jamieson, 1993; Buckland-Nicks et al., 2000). The functions of paraspermatozoa have been reviewed by Buckland-Nicks (1998; Buckland-Nicks et al., 1999). Eertman (1996) described the ultrastructure of the gill filaments of *L. articulata*.

## MATERIAL AND METHODS

Shell dimensions were measured with vernier calipers to 0.1 mm. Shell height (H) is the maximum dimension parallel to the axis of coiling, shell breadth (B) the maximum dimension perpendicular to H, and the length of the aperture (LA) the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. Shell shape was quantified as the ratio H/B and H/LA (relative spire height, SH).

For general accounts of the male and female anatomy of *Littoraria*, and methods of study, see Reid (1986a; 1999a). Living animals were relaxed in 7.5% magnesium chloride in fresh water, fixed in 10% seawater formalin and stored in 80% ethanol before examination. Paraspermatozoa were examined from the seminal vesicles of specimens fixed and stored in 10% seawater formalin. The relative radular length was the total radular length

divided by shell height. Radulae were cleaned by soaking in a hypochlorite bleaching solution at room temperature for about 5 min, rinsed in distilled water, mounted on a film of polyvinyl acetate glue on glass, allowed to dry in air, and coated with gold and palladium before examination in a scanning electron microscope. Unworn portions of radulae were viewed in three orientations: in standard flat view from vertically above the radula (to show shapes of teeth), at an angle of 45° from the front end of the radula (to show shapes of tooth cusps), and at an angle of 45° from the side of the radula (to show relief).

## Institutional abbreviations:

AMS, Australian Museum, Sydney  
 ANSP, Academy of Natural Sciences of Philadelphia  
 BMNH, Natural History Museum, London  
 MNHN, Muséum National d'Histoire Naturelle, Paris  
 NSMT, National Science Museum, Tokyo  
 NMW, National Museums and Galleries of Wales, Cardiff  
 RNHL, Nationaal Natuurhistorisch Museum, Leiden  
 USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.  
 ZMA, Institute of Taxonomic Zoology, University of Amsterdam

## SYSTEMATICS

*Littoraria (Littorinopsis) scabra* Linnaeus, 1758

**Distribution:** New records: Mascarene Islands: Rodrigues (NMW); Vietnam: Lo River, Nha Trang (BMNH); China: Sanya, Hainan Island (BMNH); Taiwan: Tan Shui (BMNH); Japan: Amami O Shima (Kyushu University); Iwoda, Ishigaki Shima (BMNH); Chichijima and Hahajima, Ogasawara Islands (Fukuda, 1993).

*Littoraria (Littorinopsis) lutea* Philippi, 1847

**Distribution:** New records: Vietnam: Lo River, Nha Trang (BMNH); Indonesia: Lembar, Lombok (BMNH).

*Littoraria (Littorinopsis) pallescens* Philippi, 1846

**Distribution:** New records: Vietnam: Lo River, Nha Trang (BMNH); China: Sanya, Hainan Island (BMNH); Taiwan: Tan Shui (BMNH); Japan: Naze, Amamioshima (Kyushu University); Kabria Bay, Ishigaki (BMNH).

**Figures 1–13.** Shells of *Littoraria bengalensis* new species and *Littoraria intermedia*. 1–11, *L. bengalensis*: 1, 7, Batu Maung, Penang, Malaysia (BMNH 20010115, 1, male; 7, female); 2, 4, S. Paratypes, Hare Island, Gulf of Mannar, Tamilnadu, India (BMNH 20010110; 2, 8, female; 4, male); 3, 6, Tuticorin, Tamilnadu, India (BMNH 20000753, females); 5, Sungai Merbok, near Pantai Merdeka, Kedah, Malaysia (BMNH 20010115, male); 9, Ao Nam Bor, Phuket Island, Thailand (BMNH 20010117, female); 10, Holotype, Hare Island, Gulf of Mannar, Tamilnadu, India (BMNH 20010111, male); 11, Ao Nam Bor, Phuket Island, Thailand (BMNH 20010116, male); 12, 13, *L. intermedia*: Hare Island, Gulf of Mannar, Tamilnadu, India (BMNH 20000754; 12, male; 13, female).

Western Australia: Berkeley River, W coast Joseph Bonaparte Gulf (BMNH); Mangrove Bay, Cape Range (BMNH); Mariana Islands: Merizo, Guam (BMNH).

*Littoraria (Littorinopsis) bengalensis* new species

(Figures 1–11, 14–16, 20–22, 34, 35)

*Littorina scabra*—Nielsen, 1976: 1–4, fig. 1A (in part, includes *L. scabra* (Linnaeus, 1758), *L. pallescens* (Philippi, 1846) and probably *L. intermedia* (Philippi, 1846)).

*Littoraria intermedia*—Reid, 1985: 39–68, figs 9, 11 (zonation) (fig. 9 includes *L. intermedia* (Philippi, 1846)). Cook and Garbett, 1989: 5, fig. 1c, 2c (penis) (in part, includes *L. intermedia* (Philippi, 1846)).

*Littoraria (Littorinopsis) intermedia*—Reid, 1986a: 124–135, figs 43b, 44e, f, 45c, d, 46b (penis), 16k (paraspermatozoa) (in part, includes *L. intermedia* (Philippi, 1846)).

**Etymology:** From the Bay of Bengal, of which the known distributional range of this species spans the southern part.

**Types:** Holotype BMNH 20010114 (Figure 10); 17 dry paratypes BMNH 20010140 (Figures 2, 4, 8); 100 paratypes in ethanol BMNH 20000755; 4 dry paratypes USNM 1000857.

**Type locality:** Hare Island, Gulf of Mannar, Tamilnadu, India.

**Material Examined:** 32 lots; 15 penes; 7 sperm samples; 4 pallial oviducts; 4 radulae.

**Shell (Figures 1–11):** Adult size range 12.3–25.6 mm. Shape elongate-turbinate (H/B = 1.49–1.86; SH = 1.72–2.16); whorls moderately rounded, suture impressed, periphery of last whorl angled, often with a raised rib; relatively thin-shelled. Mature lip sometimes slightly flared in males, varices rarely formed. Columella wide, pillar straight or slightly convex, excavated. Sculpture of (S)9–10 primary spiral grooves on spire whorls, equally spaced; primary grooves remain as incised lines or up to 0.2–0.3 rib width on last whorl, often slightly deeper and wider posteriorly (where occasionally posterior groove may be 0.5–1 rib width); intervening ribs remain undivided until last whorl, where 2–4 posterior ribs (excluding rib adjacent to suture) become divided by a central impressed line; peripheral rib usually raised, occasionally carinate; sometimes a narrow riblet interpolated in 2–3 posterior grooves; basal ribs finer; total ribs on last whorl 21–35. Surface glossy, spiral microstriae faint or absent. Protoconch 0.35 mm diameter, 3.5 whorls, with spiral ribs and sinusigera notch. Color variable; ground color cream, pale yellow or ochre; pattern of dark brown dashes on ribs, on spire whorls dashes are usually axially aligned to form oblique or zigzag stripes, but on last whorl dashes become less discrete and break up into diffuse blackish to red-brown mottling; often a broad paler zone on middle of base; pattern sometimes faint, so that shell appears yellow with grey-brown mottling. Columella purple brown to dark violet; aperture with exterior pattern showing through and not obscured by the thin whitish callus.

**Animal:** Headfoot, operculum, pallial oviduct and radula (Figures 34, 35) do not differ significantly from those of *L. intermedia* as described by Reid (1986a). Penis (Figures 14–16, 20) bifurcate; large dark brown glandular disc carried on long branch of base; smooth blade-shaped filament with mucronate tip, separated from wrinkled base by constriction, 0.4–0.5 total length of penis; entire vas deferens from tip of penial filament to prostate closed as a duct. Paraspermatozoa (Figure 21; Reid, 1986a: fig 46k) 14–26  $\mu$ m (including rod pieces); rod pieces composed of a bundle of several narrow elements, or rarely single, usually projecting from cell; cell filled with large round granules. Oviviviparous; embryos brooded between gill folds in mantle cavity until veliger stage; development planktotrophic.

**Distribution:** Habitat on branches and foliage of mangroves (*Avicennia*, *Rhizophora*, *Sonneratia*) and maritime trees (*Pemphis*), up to 3.5 m above ground, always above water level; most frequent at seaward edge of mangrove forests, but extending far back into forest (see Reid, 1985: figs 9, 11, for zonation; as *L. intermedia*); only rarely found on rocks. Found in moderately turbid and estuarine localities as well as on nearshore islands. Range (Figure 22) from India to western Malay Peninsula and northern Sumatra. Records: India: Chaiapati Beach, Mumbai (USNM); Vengurla (USNM); Mandovi Estuary, Goa (BMNH); Netravata R., Mangalore (USNM); Cochin Harbor (ANSP); Alleppey (BMNH); Tuticorin (BMNH, USNM); Krasadai I., Gulf of Mannar (BMNH); Portonovo, Tamilnadu (BMNH); Chennai (BMNH); Port Blair, Andaman Is (BMNH). Burma: Thavawthadangyi Kyun (Elphinstone I.), Mergui Arch. (BMNH); Kadan Kyun (King I.), Mergui Arch. (BMNH); Laubi Kyun (Sullivan I.), Mergui Arch. (BMNH). Thailand: Goh Contee, Ranong (MCZ); 70 km S Ranong (BMNH); Ao Nam Bor, Phuket I. (BMNH); Pulau Tiga, Butang Is (USNM). Malaysia: Merbok Estuary (BMNH); Batu Maning, Penang (BMNH); Matang Estuary (BMNH). Indonesia: Belawan, Deli, Sumatra (RNHL); Sibabang, Simenluë I. (RNHL).

**Remarks:** In his discussion of *L. intermedia* Reid (1986a: 134) noted that specimens from southwestern Thailand, Penang and India had thin-walled, often large shells with an irregular color pattern. This form occurred together with typical *L. intermedia* at Phuket Island, Thailand, yet was not considered distinct, since it was claimed that intermediates were present and because no anatomical differences were observed. Although the shells can be closely similar and anatomical differences are slight, new evidence supports recognition of this form as a distinct species. This was first suggested by field observations at the type locality (Hare Island, Gulf of Mannar). Here, three species occurred together on shrubs of *Pemphis* overhanging a sheltered sandy lagoon behind a fringing reef. There was a clear zonation: *L. intermedia* was present on trunks at a level of 0–30 cm above the high water mark; *L. scabra* occupied a zone 30–60 cm above high water, on trunks and branches,

whereas a third species (*L. bengalensis*) occurred on both foliage and branches from a height of 30–100 cm. The three species could be separated by shell characters (see below) and, most significantly, all three were copulating only with conspecifics. Subsequent anatomical examination found a consistent difference in the penis of *L. bengalensis* and *L. intermedia*. Reexamination of museum collections has revealed sympatric occurrence (mixed samples) of *L. bengalensis* and *L. intermedia* at the following additional localities: Galle, Sri Lanka (BMNH); two islands in Mergui Archipelago, Burma (BMNH); Ao Nam Bor, Phuket I., Thailand (BMNH); Pulau Tiga, Butang Is., Thailand (USNM); Sinabang, Simeulue I., Indonesia (RNHL). In each case separation of shells was straightforward, with no intermediates, and males from Ao Nam Bor were also distinguished using the same penial characters as at the type locality.

The differences between *L. bengalensis* and *L. intermedia* are summarised in Table 1. The shells of *L. intermedia* show considerable geographical and ecotypic variation (see Reid, 1986a, and below), so the descriptions apply only to specimens from within the geographical distribution of *L. bengalensis* and from the mangrove habitat. For comparison, shells of *L. intermedia* from the type locality of *L. bengalensis* are illustrated (Figures 12, 13). The shells of *L. bengalensis* are usually larger, up to 28.6 mm, those of *L. intermedia* rarely exceeding 18 mm (although the maximum size of the species as a whole is actually greater, 32 mm; Reid, 1986a). They are also of thinner texture, with more sharply angled periphery, than those of *L. intermedia*. Sexual dimorphism is evident in both species (Figures 1–13), males being smaller and with a relatively lower spire and larger aperture (Reid, 1986a); however, males of *L. bengalensis* often have a more elongately patulous shape, reminiscent of a *Succinea* (compare Figures 5 and 12). The overall color of the shell is ochraceous or yellowish, with brown pattern, in *L. bengalensis*; in contrast, that of *L. intermedia* is grey with black to brown pattern. In detail, the dark pattern of dashes on the ribs is similar on the early whorls of both species, but on the final whorl the dashes of *L. intermedia* remain more discrete and axially aligned, whereas in *L. bengalensis* the pattern becomes more diffuse and mottled. In both species there appears to be a direct effect of substrate upon shell color, presumably mediated through diet (Reid, 1986a). Shells from *Rhizophora* and *Pemphis* are darkly patterned, whereas those from *Avicennia* and *Sonneratia* are conspicuously paler. Only *L. intermedia* is known to occur on rocks and these too are usually relatively pale in color.

The only anatomical difference that has been observed is the shape of the penis: that of *L. bengalensis* has a more robust filament and a larger glandular disc borne on a longer branch of the base (although the proportions of the penis depend upon the degree of relaxation, see Reid, 1986a; fig. 46). In all animals examined the penial glandular disc of *L. bengalensis* was dark brown, whereas that of *L. intermedia* was cream or yel-

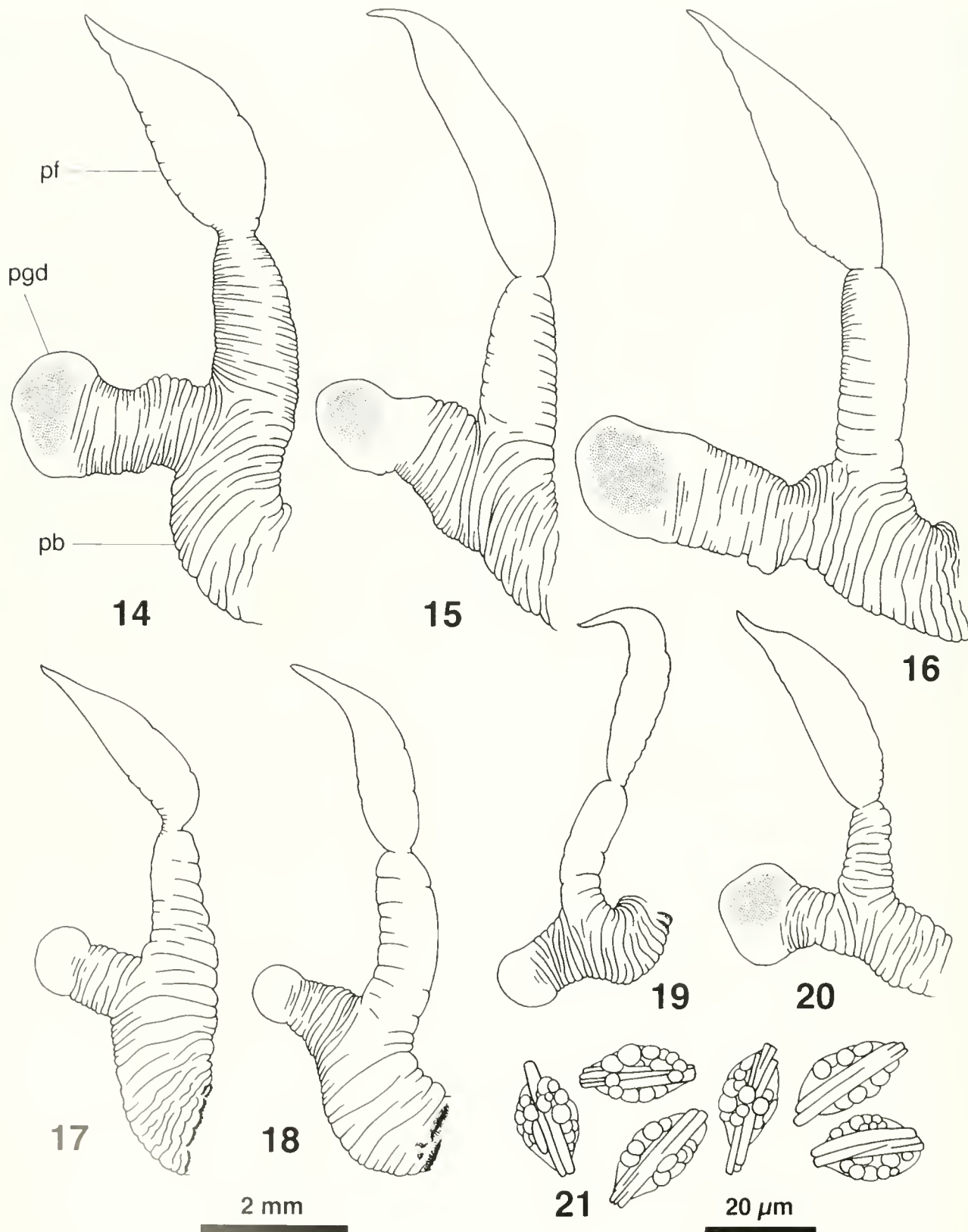
lowish. There may also be a difference in the paraspermatozoa: in *L. bengalensis* the rod pieces usually project

(Figure 21; Reid, 1986a; fig. 46k), but in *L. intermedia* they seldom pierce the oval outline of the cell (Reid, 1986a; figs 46i, j) based on 7 and 5 samples respectively.

There is little information on the comparative habitats of *L. bengalensis* and *L. intermedia* since the two have only recently been distinguished in the field and found in sympatry. The available observations indicate that *L. bengalensis* is found higher on the trees, throughout a greater width of the mangrove forest and that it is more tolerant of turbid and estuarine conditions. For example, at the muddy bay of Ao Nam Bor, Phuket Island, Reid (1985; fig. 9) recorded *L. intermedia* from throughout a mangrove stand 80 m wide, through to the landward zone and at heights of up to 3.5 m above the ground. Both species are present at this site (collections of Reid in BMNH) and since in other parts of its range *L. intermedia sensu stricto* is known to occur mainly at the seaward edge and at low levels on trees, it is likely that the high-level and landward records apply to *L. bengalensis*. At the muddy, turbid site of Batu Maung, Penang, only *L. bengalensis* was present and here Reid (1985; fig. 11, as *L. intermedia*) recorded it from throughout a belt of *Avicennia* 10 m wide and from up to 2.0 m above the ground. Likewise in the nearby Merbok Estuary *L. bengalensis* occurred alone and from seaward edge to landward fringe (personal observation). The type locality of *L. bengalensis* is a sandy island with a fringing reef and clear water: here both species occurred and *L. bengalensis* was found above the level of *L. intermedia* and on both foliage and branches, whereas the latter was present only on trunks and has rarely been found on leaves elsewhere (Reid, 1985). *Littoraria bengalensis* has so far been recorded almost exclusively on trees (one specimen on a sheltered rocky shore near Ranong, Thailand; BMNH), whereas *L. intermedia* is commonly found on both trunks and sheltered rocky shores (Reid, 1985; 1986a).

Reid (1986a: 57–58) discussed a distinction between *Littoraria* species with 'oceanic' and 'continental' distribution patterns, representing extremes on a gradient of ecological tolerance. The former referred to a suite of habitat characteristics including clear water, normal salinity, narrow mangrove fringes or seaward edges of broad mangrove belts, and offshore islands. In contrast, 'continental' habitats were characterised by turbid, estuarine water, eutrophic conditions, and broad forests on continental margins. It is clear that on this continuum *L. bengalensis* extends to more 'continental' habitats than *L. intermedia*. For example, in the Andaman Sea both species have been recorded from the Andaman Islands, Mergui Archipelago, Phuket Island and Butang Islands (details given above); these are all 'oceanic' sites. However, at a muddy site on Penang and in both the Merbok and Matang Estuaries, and in the vicinity of Ranong, on or close to the mainland of the Malay Peninsula, *L. bengalensis* occurred alone (large collections





by D.G. Reid, E. Ashton and J.D. Taylor respectively; all BMNH). Similarly, in India *L. bengalensis* has been recorded over a large extent of the continental coastline, from Mumbai to Chennai, from islands in the Gulf of Mammur and from Galle in Sri Lanka. In contrast, in the same region *L. intermedia* has been recorded only from islands in the Gulf of Mammur, from Galle and from Trincomalee, Sri Lanka (see below), all of which appear to be 'oceanic' sites. On a wider geographical scale the distribution of *L. intermedia* extends across the Pacific to the islands of Hawaii and Polynesia, again reflecting the 'oceanic' character of this species.

The northern limits of *L. bengalensis* in the Bay of Bengal are not clear, owing to the few available collections from northeastern India and Bangladesh. So far, only two *Littoraria* species have been recorded from Bengal and Bangladesh, *L. delicatula* and *L. melanostoma* (Reid, 1986a; see below).

The many morphological similarities between *L. bengalensis* and *L. intermedia* leave little doubt that the two are sister species. Likely synapomorphies include the blade-shaped penial filament with mucronate tip and the bundles of narrow rod-pieces in the paraspermatozoa, both unique in the genus. The closed penial vas deferens is a likely synapomorphy of a clade comprising *L. bengalensis*, *L. intermedia*, *L. subittata* Reid, 1986 and *L. philippiana* (Reeve, 1857) (Reid, 1999b).

Confusion of *L. bengalensis* with other species is less likely. In southern India and the southern Andaman Sea its range overlaps with that of *L. scabra* and the two can be found sympatrically in relatively 'oceanic' habitats (including the type locality in the Gulf of Mammur). *Littoraria scabra* is easily recognised by its wide, white columella. *Littoraria pallescens* (Philippi, 1846) is even more oceanic in character than *L. scabra* and has been recorded sympatrically with *L. bengalensis* only in the Andaman Islands, Penang, Butang Islands and Phuket Island; it is distinguished by its colorful, polymorphic shell, lack of secondary sculpture and the rounded inner lip of the aperture. In each case penial characters are diagnostic (Reid, 1986a). The distribution of *L. bengalensis* just touches that of *L. delicatula*, single specimens of the latter having been seen from the Gulf of Mammur and the Andaman Islands, although most are from the head of the Bay of Bengal (see below). Shells of these two species can be superficially similar: both may be thin-shelled, and yellow with a faint or diffuse pattern. Nevertheless, they can always be distinguished by the

more numerous primary grooves (11–11) and much finer sculpture (35–50 ribs on final whorl) of *L. delicatula*; the columella of that species is narrow and excavated in the typically very delicate shells, although it may approach that of *L. bengalensis* in width in occasional thicker shells. The shape of *L. delicatula* is subtly different; the spire whorls are flatter and the spire usually slightly taller. Most importantly, the penis of *L. delicatula* is entirely different (Figures 31, 32, see below).

*Littoraria* (*Littorinopsis*) *intermedia* (Philippi, 1846) (Figures 12, 13, 17–19, 22)

Synonymy as in Reid (1986a), excluding the entries now listed under *L. bengalensis* above. New references:

*Littoraria* (*Littorinopsis*) *intermedia* Reid, 1986a: 124–135, figs 43a, c–i, 44a–d, g–i, 15a, 15b (protoconch), e, 15f (radula), 46a, c–h (penis), 46i, j (paraspermatozoa), 46l–o (oviduct), 47 (distribution) (in part, includes *L. bengalensis* new species).

**Distribution:** Records and distribution as in Reid (1986a: 132–134, fig. 47), but excluding all records from mainland India except those listed below, and also excluding records from Penang, Merbok estuary and Belawan (the excluded records apply to *L. bengalensis*, see above). The doubtful record from the Galápagos Islands (Reid, 1986a: 134) is now considered unreliable and should be excluded (Reid and Kaiser, 2001). New and reconfirmed records: Kenya: Kilifi R. estuary (BMNH); Saudi Arabia: Jeddah (BMNH); Oman: Masirah I. (ZMA); Khor Al-Jaruma, Ras Al-Hadd (BMNH); Bandar Khayran (BMNH); United Arab Emirates: Fujaira (BMNH); Ras Al-Khaimah; Khor, Dubai (BMNH); Khor Kalba, Sharjah (BMNH); India: islands in Cochin Harbour, Kerala (ANSP); Manali I. and Hare I., Gulf of Mammur (BMNH); Thailand: Krabi (BMNH); Malaysia: Pulau Gaya, Kota Kinabalu, Sabah (BMNH); Kudat, Sabah (BMNH); Vietnam: Lo R., Nha Trang (BMNH); China: Beigang I., Hainan (BMNH); Indonesia: Kuta Beach, Lombok (BMNH); Philippines: Mandalay, S. El Nido, N. Palawan (BMNH); Taiwan: Tan Shui (BMNH); Japan: Ishigaki (BMNH); Yakushima, S. Uozumi Colln.; Amamioshima, S. Uozumi Colln.; Shirahama, Wakayama (BMNH); Chichijima, Ogasawara Islands (Fukuda, 1993); Australia: Wooli Wooli R., New South Wales (AMS); Tonga: Sopo, Nukunolofa, Tongatapu (BMNH).

**Remarks:** Reid (1986a) characterised this as a typi-

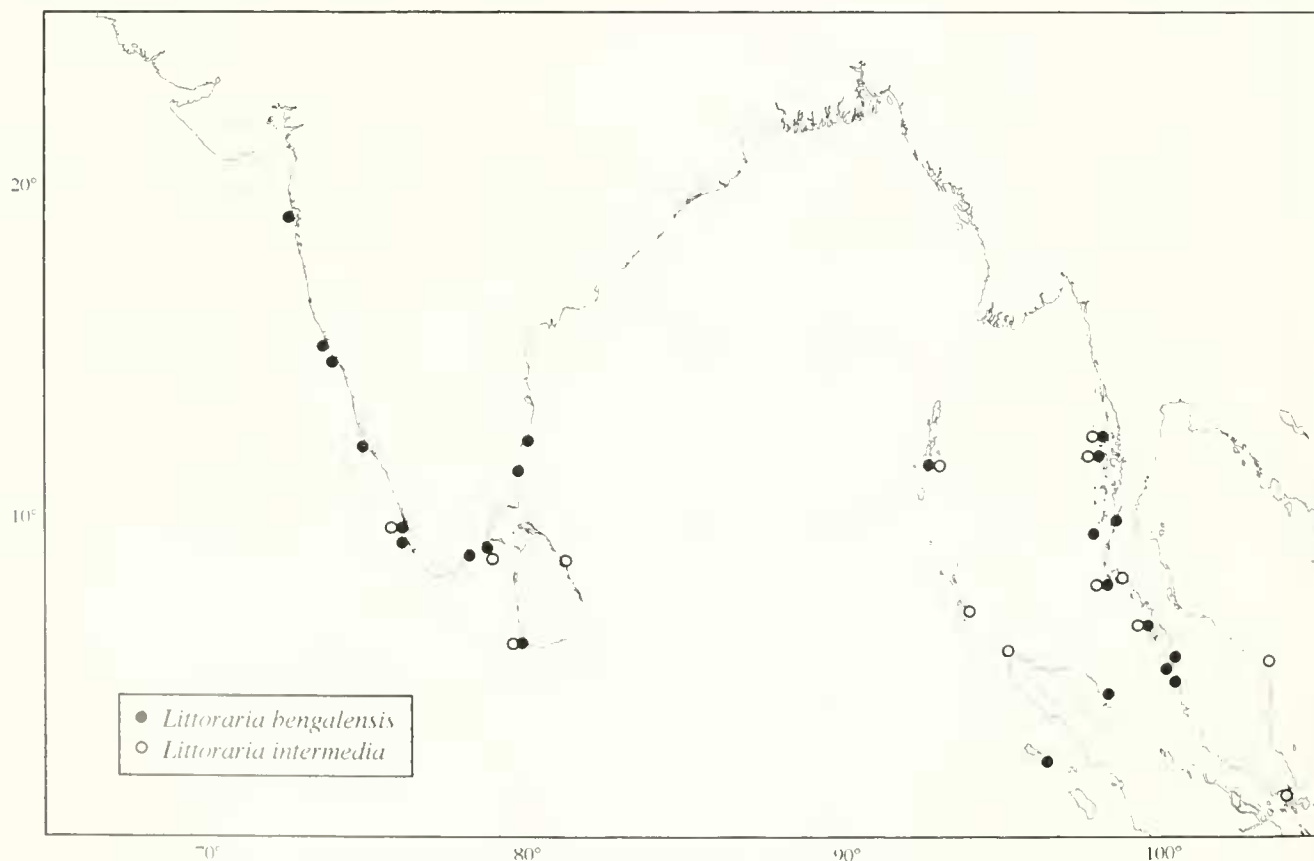
**Figures 14–21.** Penes and paraspermatozoa of *Littoraria bengalensis* new species and *Littoraria intermedia*. **14–16.** Penes of *L. bengalensis*. **14–16.** Paratypes: Hare Island, Gulf of Mammur, Tamilnadu, India (BMNH 20000755; shell H = 17.0 mm, 16.4 mm, 16.6 mm). **20.** Ao Nam Bor, Phuket Island, Thailand (BMNH 20010116; shell H = 13.0 mm). **17–19.** Penes of *L. intermedia*. **17, 18.** Hare Island, Gulf of Mammur, Tamilnadu, India (BMNH 20000754; shell H = 12.8 mm, 15.3 mm). **19.** Ao Nam Bor, Phuket Island, Thailand (BMNH 20010119; shell H = 13.4 mm). **21.** Paraspermatozoa from one paratype of *L. bengalensis*: Hare Island, Gulf of Mammur, Tamilnadu, India (BMNH 20000755). Abbreviations: pb, penial base; wrinkled, pl, penial filament; smooth, pgd, penial glandular disc. Stipple on penial glandular disc indicates dark brown coloration, shading at base of penis indicates black pigment in epithelium.

**Table 1.** Summary of differences between *Littoraria bengalensis* new species and *L. intermedia* (shell characters apply to specimens from mangrove habitats in northeastern Indian Ocean only).

Character	<i>Littoraria bengalensis</i>	<i>Littoraria intermedia</i>
Shell shape	Larger (to 29 mm), thinner texture, peripheral angulation with raised rib	Smaller (to 18 mm), more solid, more rounded periphery
Shell color	Ochre to yellow, with brown pattern; on last whorl the dark dashes are diffuse	Grey, with black to brown pattern; on last whorl the dark dashes remain discrete and axially aligned
Penis	Robust filament; brown glandular disc borne on long branch of base	More slender filament; cream glandular disc borne on shorter branch of base
Paraspermatozoa	Rod pieces project from cell	Rod pieces seldom project from cell
Habitat	More tolerant of turbid and estuarine conditions; occurs higher on trees and throughout forest; found on trunks, branches and foliage, rarely on rocks	Preference for clear water; found lower on trees and only common at seaward edge of forest; found on roots, trunks and sheltered rocks
Distribution	Northeastern Indian Ocean, from India to western Malay Peninsula and northern Sumatra	Occurs widely throughout Indo-West Pacific region

eally oceanic species, with a wide distribution from South Africa to the Red Sea, throughout the Indo-West Pacific tropics to Hawaii and Polynesia. Within this area he pointed out three distinctive geographical forms, from the central Pacific, from the western Indian Ocean (including the Red Sea) and from India and the Andaman Sea. It is demonstrated above that the last of these

is a distinct species, *L. bengalensis*. Its recognition removes the anomaly of the occurrence of this 'form' in the relatively continental conditions of broad mangrove forests in estuaries on the mainland shores of the western Malay Peninsula. An obvious question is whether the other 'forms' might also deserve specific status. Accordingly, much new anatomical material has been examined



**Figure 22.** Geographical distribution of *Littoraria bengalensis* with, for comparison, the records of *Littoraria intermedia* from the same area (see text for lists of records).



from throughout the range of this species, in particular 66 penes have been drawn. However, no obvious discontinuities have been found. Furthermore, in areas such as the Solomon Islands, New Caledonia and Fiji, where overlap in the ranges of a putative Indo-Malay species (the 'typical form') and a putative central Pacific species might have been predicted, no evidence has been found for the sympatric occurrence of discrete conchological or anatomical types. Instead, the evidence continues to suggest a single widespread species, typical of oceanic habitats, in which shell characters show small and gradual changes (in the color pattern, frequency of color morphs, and presence of secondary sculpture) across the considerable geographical range. Shell characters continue to show a strong correlation with habitat as well as geography, as pointed out by Reid (1986a). Thus, throughout the range, those specimens from rocky shores (and from certain mangrove tree species such as *Avicennia* and *Sonneratia*) are paler in color and show a more diffuse pattern, in comparison with the typically dark shells found on *Rhizophora* trees, which are the prevalent shell type in the Indo-Malay and Australian regions.

The new records listed above significantly extend the known range of this species in Arabia, the South China Sea, and southeastern Australia. In Japan, the record from Shirahama confirms the (presumably sporadic) occurrence of this species in the Kii Peninsula (the record in Reid, 1986a, was based on a shell illustrated by Habe, 1964). Additional collecting in northwestern Australia (M. Stuckey, personal communication) has failed to find this species further west than the Coburg Peninsula, so its absence from Western Australia appears to be real.

*Littoraria (Littorinopsis) subvittata* Reid, 1986a

**Distribution:** New record: Mascarene Islands: Rodrigues (NMW).

*Littoraria (Littorinopsis) philippiana* (Reeve, 1857)

**Distribution:** New records: New South Wales: Wooli Wooli River (AMS).

*Littoraria (Littorinopsis) filosa* (Sowerby, 1832)  
(Figures 23–30)

**Animal:** Penis (Figures 23–30): in specimens from Western Australia the glandular limb is often longer and more robust than previously reported (Reid, 1986a: fig. 54); it may be as long and up to 3 times as broad as the penial filament.

**Distribution:** New records: Northern Territory: Forsyth Creek, E coast Joseph Bonaparte Gulf (BMNH); Western Australia: Berkeley River and Revelly Island, W coast Joseph Bonaparte Gulf (BMNH).

**Remarks:** Reid (1986a) noted that the geographical form found from Cape Leveque to Exmouth Gulf in

Western Australia differed from the typical form on the east and north coast of Australia by more numerous but less prominent primary ribs and by details of color pattern. Taxonomic recognition was not considered justified since no anatomical differences were detected. New material from throughout the range in Western Australia (including the two listed above that fill in a gap in the known distribution) confirms the reported shell differences, but adds some significant details. The typical carinate (eastern) shell type extends to both localities in Joseph Bonaparte Gulf listed above, whereas a large sample (about 100, BMNH) from Cape Leveque displays characteristics intermediate between eastern and western shells. The western forms often, but not always, have penes with an unusually long and robust glandular branch of the base, exceeding in size any seen from northern or eastern Australia (samples of 30 western and 55 eastern penes). In none of the samples from Western Australia or Northern Territory is there any morphological evidence for a mixture of two discrete shell types with correlated penial differences. The earlier taxonomic conclusion therefore seems justified from a morphological viewpoint, and the evidence appears to show a blending of characters between two forms with a continuous distribution, rather than allopatry or limited overlap between two distinct forms. However, this interesting case should be investigated with genetic techniques (presently being done by M. Stuckey, University of Western Australia).

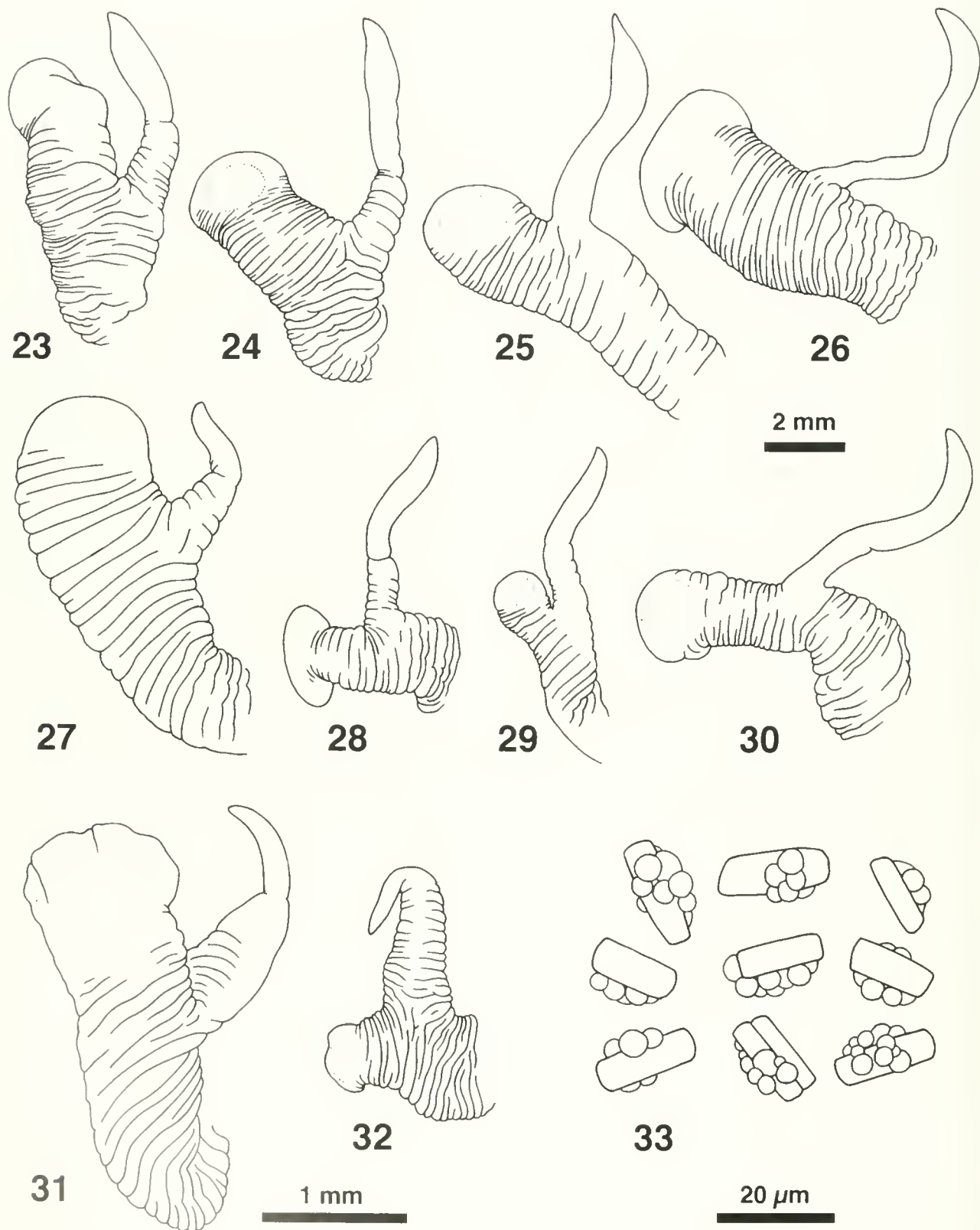
The apparent trend towards a longer glandular branch in the penis of the western form of *L. filosa* might repay further investigation. It could be significant that the eastern form (with relatively shorter glandular branch) is broadly sympatric with *L. philippiana*—a congener with a much longer glandular branch. In contrast the western form (with relatively longer branch) is largely sympatric with *L. cingulata*, in which penial shape is more similar to that of the eastern form of *L. filosa* (see Reid, 1986a: figs 41, 58). If penial shape is a species recognition character, its variation within *L. filosa* might suggest a case of character displacement.

*Littoraria (Littorinopsis) ardouiniana* Hende, 1885

**Distribution:** New records: Taiwan: Tan Shui, China; Sanya, Hainan, Vietnam: Sui Sot Cave, Ha Long Bay; Lo River, Nha Trang, Singapore; Changi South (all BMNH).

*Littoraria (Littorinopsis) delicatula* Nevill, 1885  
(Figures 31–33, 36, 37)

**Animal:** Penis (Figures 31, 32) bifurcate; glandular disc large, with thin margin; filament small, 0.2 total length of base, separated from wrinkled base by constriction; sperm groove open. Paraspermatzoa (Figure 33): 14–20 µm, oval, 1 (rarely 2) large rectangular rod piece filling cell; granules large, few, distinct (observation of single sperm sample preserved in 80% ethanol).



which may cause shrinkage of about 20% (Reid, 1996: 6). No data on female. Radula (Figures 36, 37): relative length 0.76; rachidian tooth: base flared, central cusp shield-shaped, small cusp and one denticle on each side; lateral tooth: 5 cusps, largest central cusp blunt; inner marginal tooth: 4 cusps; outer marginal tooth: 5 cusps.

**Distribution:** Habitat: foliage of *Aricemia alba* on muddy river bank; water of low salinity (from 2–3‰ in wet season to 16.8‰ in dry season) (G. Pendred, personal communication). New records: Bodra Kaal, Chaylabogi, Sundarbans, Bangladesh (BMNH); Krasadai Island, Gulf of Mamar, India (BMNH).

**Remarks:** Reid (1986a) did not have access to any preserved specimens, but since then two males have been dissected and one radula prepared. Based on some similarity of shells, Reid (1986a) suggested that *L. delicatula* was most closely related to *L. ardoniniana* and that anatomical evidence was required to confirm that they were indeed distinct. The newly described penial form is sufficiently different from that of *L. ardoniniana*, in which the filament is large (up to half total length of penis; Reid, 1986a) to leave no doubt that the two are separate species. The paraspermatozoa are similar in both. The penis of *L. delicatula* does not differ significantly from that of *L. pallescens* and the radulae of these species are also closely similar. Radular tooth form is not, however, a reliable taxonomic character in *Littoraria* (Reid and Mak, 1999). Despite the penial similarity *L. delicatula* is believed to be distinct from *L. pallescens*, since the shells are very different (delicate, with 11–14 primary grooves, 35–50 ribs on last whorl and narrow columella in *L. delicatula*; solid, with 9–10 primary grooves, no secondary sculpture and broad columella in *L. pallescens*; see Reid, 1986a). Paraspermatozoa also differ, being rounded with small rod pieces in *L. pallescens* (although only a single sample has been seen in *L. delicatula*). These two have not yet been collected together, but both have been recorded from the Andaman Islands (Reid, 1986a), so that the conclusion that they are distinct might be tested in future. There is a superficial similarity to *L. bengalensis* (see above).

The new record from the Gulf of Mamar greatly increases the known range of this species, previously recorded only from Port Canning (Bengal) and the Andaman Islands. It is likely, however, that the center of distribution is the northern Bay of Bengal. Only single shells are available from the Andaman Islands (BMNH; Reid, 1986a) and the Gulf of Mamar. The latter was

collected in 1931 by R. Winckworth; the species was not found on a recent visit to the Gulf of Mamar (personal observation, 2000) and is presumably rare in this area.

*Littoraria* (*Palustorina*) *melanostoma* (Gray, 1839)

**Distribution:** New records: Japan: Miyako Island; Yaeyama Islands (Higo et al., 1999).

**Remarks:** Reid (1986a) recorded the rare occurrence of a pinkish orange morph in this normally monomorphic species. This has now been seen in two samples from localities in Ha Long Bay, Vietnam (BMNH): the frequency was low (2% and 5%,  $N = 21$  and 11) and in each case the specimens were collected among saltmarsh grass (see Remarks on *L. carinifera*).

*Littoraria* (*Palustorina*) *carinifera* (Menke, 1830)

**Shell:** Two cases of color polymorphism have been recorded in this species, hitherto thought to be rather constant in coloration (Reid, 1986a). In a sample of 78 shells from Lembar, Lombok (BMNH), most had a cream to grey ground color with red brown pattern, but in seven shells (9%) the ground color was orange. The sample was collected on trunks of dwarf *Aricemia* and *Sonneratia* trees 1 m in height on a muddy foreshore. A second polymorphic sample was collected among saltmarsh grass 70 km south of Ranong, Thailand (BMNH). Here the shells were of the small, smooth form (e.g. Reid, 1986a; fig. S21); the range of colors was similar and three (6.5%) of 16 shells were orange.

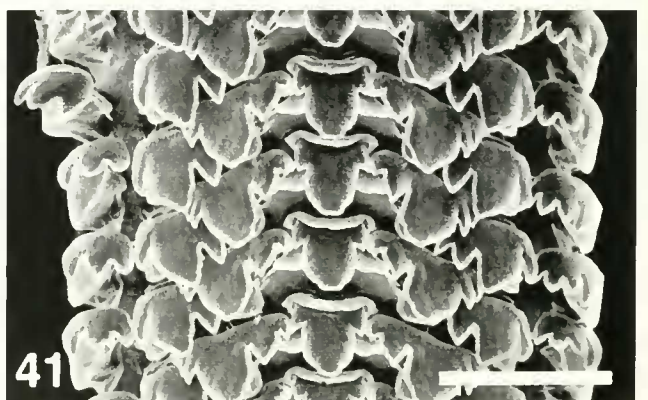
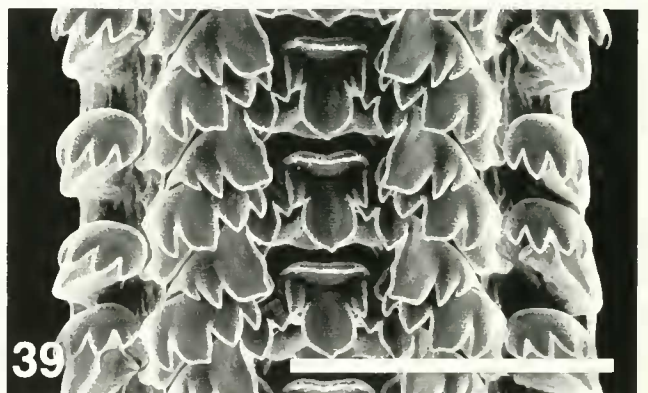
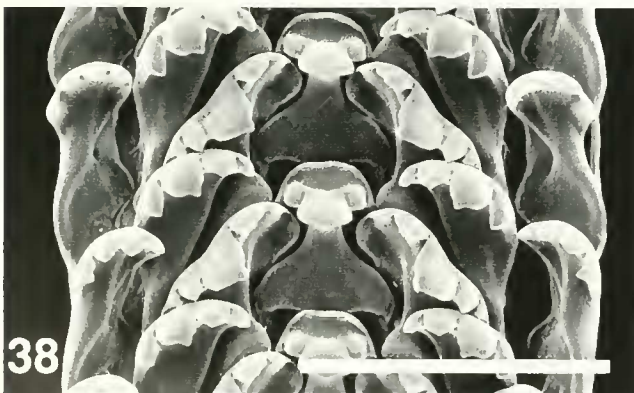
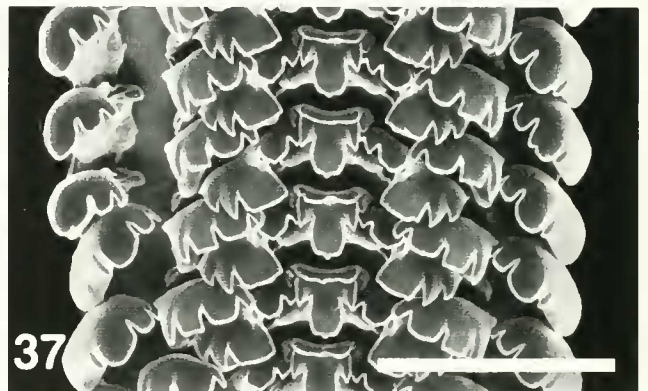
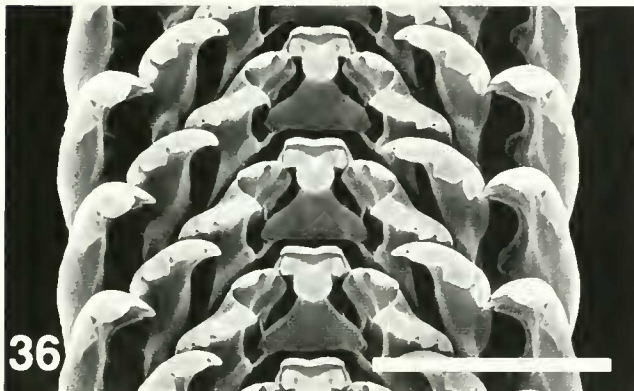
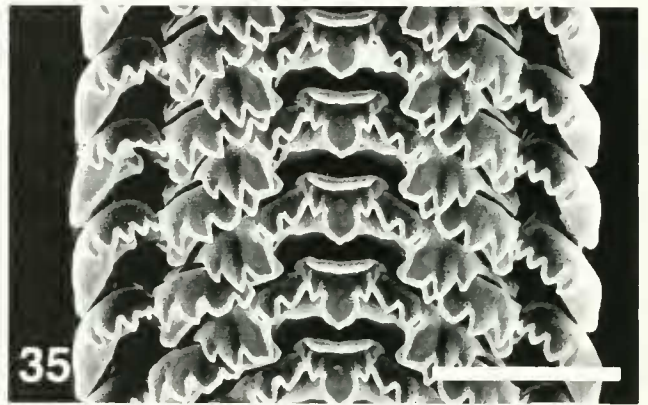
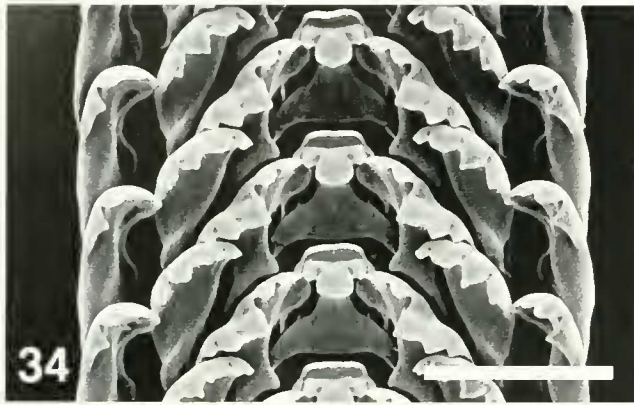
**Distribution:** New record: Indonesia: Lembar, Lombok (BMNH).

**Remarks:** Elsewhere in the subgenus *Palustorina* pinkish orange shells are very rarely encountered in *L. articulata* and *L. melanostoma*, although this morph is widely distributed (though always at low frequency) in polymorphic members of the subgenus *Littorinopsis*. *Littoraria carinifera* is normally found on trunks at low levels (up to 0.5 m) on trees in the landward fringes of mangrove forests (Reid, 1986a: 192) and shells from this habitat are of overall dark brown color and not polymorphic or variable. It may be significant that both polymorphic samples are from foliage in open sunny conditions, in other words from visually varied microhabitats where the animals might be exposed to visual predation (e.g. by birds or crabs). It is under exactly these conditions that the polymorphic species of the subgenus *Lit-*

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**Figures 23–33.** Penes and paraspermatozoa of *Littoraria filosa* and *Littoraria delicatula*. 23–30. Penes of *L. filosa*. 23–26. Julago Beach, Cape Leveque, Western Australia (BMNH 20010120; shell H = 20.5 mm, 20.5 mm, 19.5 mm, 18.7 mm). 27, 29. Lookout Hill, Broome, Western Australia (BMNH 20010121; shell H = 19.7 mm, 15.8 mm). 28. Mangrove Point, Roebuck Bay, Broome, Western Australia (BMNH 20010122; shell H = 21.1 mm). 30. Witnell Bay, Burmp Peninsula, Western Australia (BMNH 20010141; shell H = 18.3 mm). 31–33. Penes and paraspermatozoa of *L. delicatula*. Bodra Kaal, Chaylabogi, Sundarbans, Bangladesh (BMNH 20010123; shell H = 14.4 mm, 11.3 mm). Dotted line indicates extent of opaque glandular portion of penial glandular disc.





*torinopsis* occur and for which visual selection by predators has been suggested as a possible explanation for the maintenance of the polymorphism, which is assumed to have a genetic basis (Cook, 1986a, b, 1992; Reid, 1987). The same process could possibly maintain these rare, local cases of polymorphism in the normally monomorphic *L. carinifera*; a similar explanation has been proposed for local polymorphism in *L. intermedia* by Cook and Bridle (1995). However, it should be noted that like almost all others in the genus, this species has planktotrophic development and therefore the potential for wide gene flow; selection on local populations would therefore have to be strong, or gene flow would have to be restricted in some way, in order to achieve local genetic differentiation of polymorphic populations. A similar case of local polymorphism has been found in *L. melanostoma* (see above).

*Littoraria (Palustorina) sinensis* (Philippi, 1847)  
(Figures 35–52, 56–64, 68)

*Littorina sinensis* Philippi, 1847: 16–17, *Littorina* pl. 6, fig. 23 (China: lectotype (Reid, 1986a) MNHN + 2 paralectotypes, seen, Figures 42, 43). Lischke, 1871b: 71–72, Weinkanfl, 1882: 83–84, pl. 11, figs 9, 12.

*Littorina intermedia* var. *sinensis*—Novill, 1885: 147.

*Littorina sinensis*—Pilsbry, 1895: 62.

*Littorina strigata* Lischke, 1871a: 148–149 (Nagasaki, Japan; types lost; not *Littorina intermedia* var. *strigata* Philippi, 1846 = *Littoraria strigata*). Lischke, 1871b: 73, pl. 5, fig. 22 (not Philippi, 1846).

*Littorina strigata* (Lischke)—Pilsbry, 1895: 62 (not Philippi, 1846).

*Littorina (Melaraphis) strigata* (Lischke)—Tryon, 1887: 245, pl. 43, fig. 33 (not Philippi, 1846).

*Littorinopsis strigata* (Lischke)—Kuroda and Habe, 1952: 64 (not Philippi, 1846). Oyama and Takenura, 1961: fig. 10 (not Philippi, 1846).

*Littoraria strigata* (Lischke)—Kojima, 1958 (egg capsule; not Philippi, 1846). Azuma, 1960: 10 (not Philippi, 1846). Higo, 1973: 46 (not Philippi, 1846).

*Littoraria strigata* ("Dunker")—Yoo, 1976: 56, pl. 7, figs 18, 19 (not Philippi, 1846).

*Littoraria scabra strigata* (Lischke)—Higo and Goto, 1993: 74 (not Philippi, 1846).

? *Littorina adonis* Yokoyama, 1927: 451, pl. 51, fig. 8 (Koyasu, southern Musashi, Japan; Upper Musashino [Pliocene; Rosewater, 1970]; holotype, Geological Institute, University of Tokyo; not seen). Rosewater, 1970: 453, pl. 349, figs 8, 9.

*Littoraria adonis*—Okutani, 1986: 71, fig. unnumbered.

*Littorina (Littorinopsis) scabra scabra*—Rosewater, 1970: 456–461 (in part; not Linnaeus, 1758 = *Littoraria scabra*).

*Littorina scabra*—Cai, 1991: 51, fig. 43 (not Linnaeus, 1758).

*Littoraria (Palustorina) articulata*—Reid, 1986a: 200–209, figs 90c, e, 92h, i, penes, 93c, egg capsule, 94 (in part; not *Littorina intermedia* var. *articulata* Philippi, 1846 = *Littoraria articulata* Choe, 1992: 289–290, fig. 54 (not Philippi, 1846). Reid, 1992a: 195–197, fig. 1g (in part; not Philippi, 1846). Higo et al., 1999: 92.

*Palustorina* (sic) *articulata*—Fukuda et al., 1992: 57, pl. 9, figs 129a, b (not Philippi, 1846).

**Nomenclature:** The nomenclature of this species has suffered numerous changes. The name *Littorina sinensis* has seldom been used, most recently by Pilsbry (1895). It was redescribed as *Littorina strigata* by Lischke (1871a) and this name became familiar in various combinations in the Japanese literature of the mid-twentieth century. Rosewater (1970) combined it with some 20 other species under the name *Littorina scabra*. The Pliocene fossil *Littorina adonis* has not been examined, but is probably this species, and the name was used for Recent Japanese specimens by Okutani (1986). It has become generally known as *Littoraria articulata* following Reid (1986a), but that taxon is here shown to consist of two species. As discussed below, the only entirely diagnostic character is the penis, although the majority of shells can be confidently identified. Although the lectotype is a dry shell, the form of the aperture and columella, and the diffuse color pattern on the shoulder region, are typical of the present species.

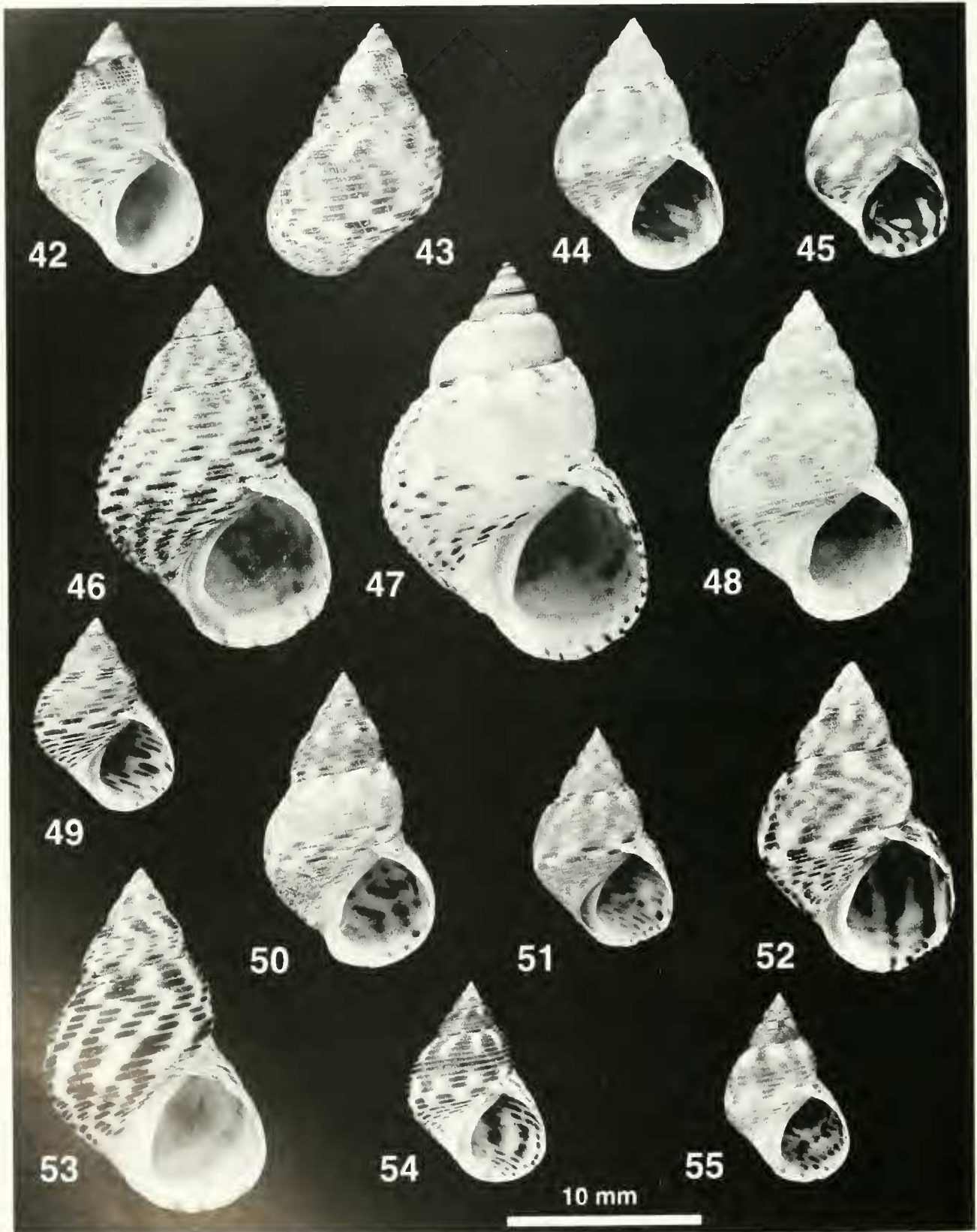
**Material Examined:** Types as indicated: 44 lots; 35 penes; 1 sperm sample; 12 pallial oviducts; 5 radulae.

**Shell (Figures 42–52):** Adult size range 6.3–20.6 mm. Shape high-turbinate to elongate (H/B = 1.28–1.73; S/H = 1.57–2.05); whorls rounded, suture impressed, periphery of last whorl slightly or not at all angled; moderate thickness. Mature lip not flared; columella pillar concave, excavated; inner lip of aperture sharply raised adjacent to base of columella. Sculpture of 17–8–9 primary spiral grooves on spire whorls; intervening ribs usually remain undivided, numbering 20–23 on last whorl; occasionally some ribs may be divided by an impressed line and become more numerous; ribs of equal width above periphery, slightly narrower on base; grooves are impressed lines on spire whorls, becoming deeper and wider on last whorl, commonly up to half width of intervening ribs at periphery of whorl (rarely equal to rib width); in smoothest shells grooves remain as impressed lines only. Microsculpture of faint spiral striae over rib surface, with axial microstriae in grooves. Protoconch 0.35 mm diameter, 3.5 whorls, with spiral

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**Figures 34–41.** Radulae of *Littoraria* species. **34, 35.** *L. bengalensis* new species; paratype: Hare Island, Gulf of Mannar, Tamilnadu, India (BMNH 20000755; shell H = 16.3 mm, flat view and 45° from anterior). **36, 37.** *L. delicatula*: Bodra Kaal, Chaylabogi, Sundarbans, Bangladesh (BMNH 20010123; shell H = 14.4 mm, flat view and 45° from anterior). **38–41.** *L. sinensis*. **38, 39.** Mangrove trees, Tan Shui, Taipei, Taiwan (BMNH 20010130; shell H = 11.4 mm; flat view and 45° from anterior). **40, 41.** Rocks, Kafuri, Maebaru City, Kyushu, Japan (BMNH 20010131; shell H = 15.5 mm; flat view and 45° from anterior). Scale bars = 100 µm.







ribs and sinusigera notch. Color variable: cream with pattern of orange brown to dark brown dashes on ribs with whitish dashes between; degree of axial alignment of dashes varies from diffusely tessellated or marbled pattern with alignment into short axial stripes at suture and periphery only (Figures 43, 44, 51) to the rare more complete alignment in oblique axial stripes (Figure 46); pattern often emphasizes 2–3 ribs at periphery. Columella purple brown or white; aperture cream with exterior pattern showing through.

**Animal:** Headfoot, operculum, paraspermatozoa, pallial oviduct and radula do not differ significantly from those of *L. articulata* as described by Reid (1986a). As in *L. articulata* (Reid and Mak, 1999: fig. 4C, D) the radula shows likely phenotypic plasticity and differs in tooth shape on rock and wood substrates (compare Figures 39 and 41). Penis (Figures 56–64) not bifurcate, small glandular disc incorporated into distal end of wrinkled base; smooth narrowly elongate filament 0.3–0.5 total length of penis; penial vas deferens an open groove to filament tip. Pelagic egg capsule a lens-shaped biconvex disc without peripheral flange, 350 µm diameter, containing single ovum about 70 µm diameter (Kojima, 1958: fig. 2a, b; reproduced in Reid, 1986a: fig. 93c). Development planktotrophic.

**Distribution:** Habitat in littoral fringe on rock (including granite boulders and concrete sea walls) in both sheltered and moderately exposed situations; also on trunks at seaward edge of mangrove forests (published accounts of the ecological distribution of *Littorina scabra* on the rocky shores of Hong Kong and southern China probably refer to a mixture of this species and *L. articulata*, e.g. Chambers, 1980; Ohgaki, 1985; Yi and Li, 1988; Yon, 1990). Range (Figure 68) from southern China to Yellow Sea, South Korea, Kyushu and Seto Inland Sea, perhaps Ryukyu Islands. Records: China: Macao (BMNH); Hong Kong (Shek O, Deep Bay; Tai Po; Three Fathoms Cove; Hoi Ha, Mirs Bay; Wu Kwai Sha, Aberdeen; all BMNH); Xiamen (Hai Gang; Gulayang; both BMNH); Spider Island, Fujian (USNM); Zhenhai, Ningbo River (BMNH); Shawaishan, mouth of Yangtze River (BMNH); Qingdao (Tai Ping; Huan Dao; Hui Quan; all BMNH). Taiwan: Tan Shui (BMNH). Japan: Ryukyu Islands (USNM); Kagoshima (BMNH); Amakusa (USNM, NSMT); Matsunra, Nagasaki Pref. (BMNH); Hirado (AMS); Maebaru City (BMNH); Ehime Pref. (USNM); Kasaoka, Okayama Pref. (USNM); Nagae River, Okayama City (BMNH); Yoshino River,

Tokushima City (BMNH). South Korea: Sachun Kim, Kyongsang Namdo (ANSP).

**Remarks:** Reid (1986a) concluded that *L. articulata* was a single species extending from Australia to India and Japan but with two geographical forms of more restricted distribution, one from northwestern Australia and the other from China and Japan. The latter was characterised by stronger sculpture, a more diffuse pattern and it was said that the penial filament was 'sometimes relatively longer than in specimens from South East Asia and Australia'. It was also noted that the egg capsule of the Japanese form described by Kojima (1958) was larger than that of *L. articulata* from Queensland and lacked the circumferential flange. However, with little information on the range of intraspecific variation the significance of the difference in capsule shape was unclear. The eastern Asian form was 'tentatively assigned to *L. articulata*', but it was suggested that further work was required.

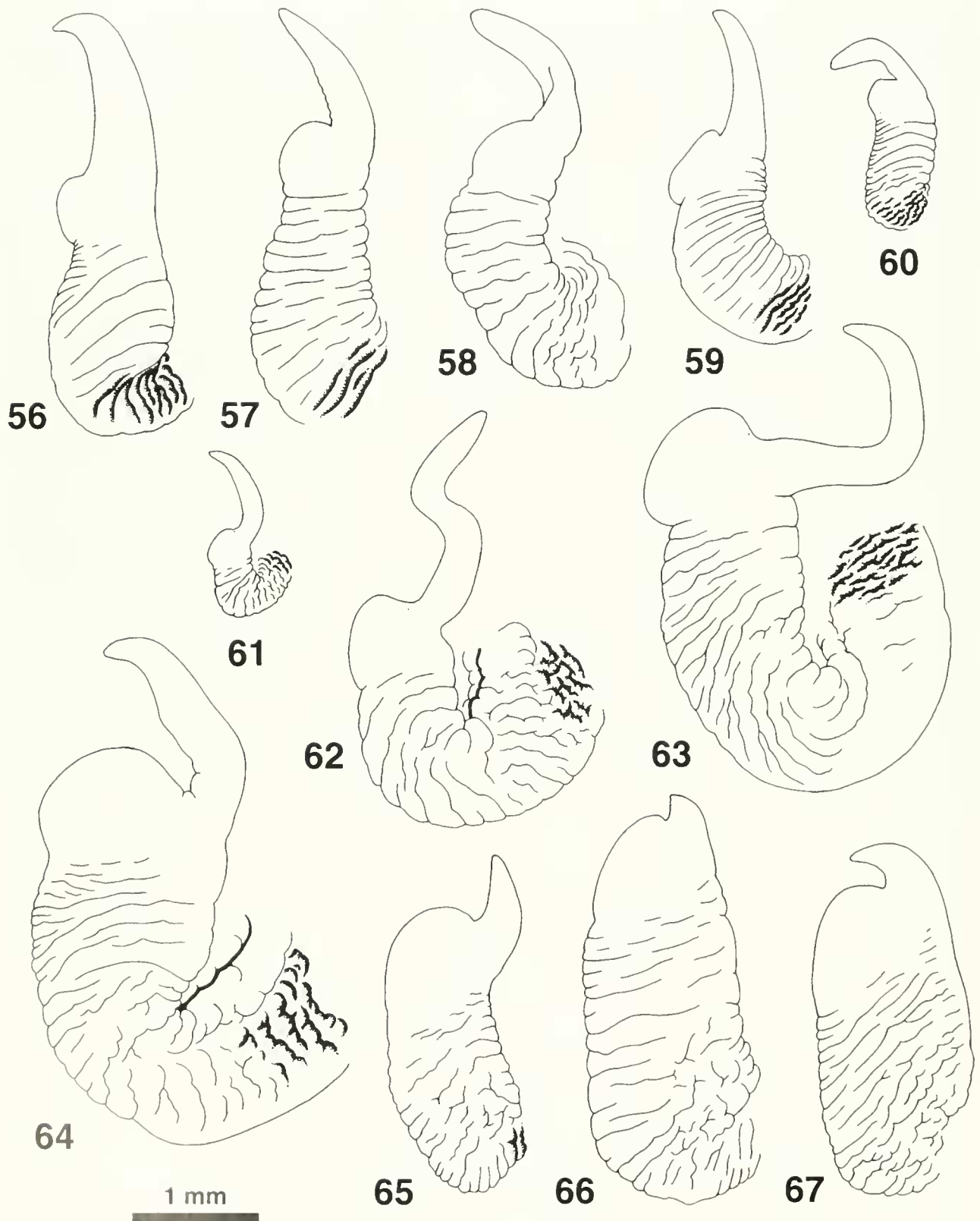
Since then, much additional material has been gathered. It has been found that all specimens from northern China, Korea and Japan share the longer penial filament. Most significant, however, is the discovery that the typical form of *L. articulata* and the eastern Asian 'form' occur syntopically at several localities in southern China, around Hong Kong and Xiamen. At these localities the penial differences remain distinct (e.g. Figures 57, 58 and 65, 66, from a locality in Hong Kong) and are correlated with small, but consistent, differences in shell shape, sculpture and color. This leaves no doubt that the 'forms' are separate species.

The differences between *L. articulata sensu stricto* and *L. sinensis* are summarised in Table 2. The most useful and entirely diagnostic character is the shape of the penis: in *L. sinensis* (Figures 56–64) the penial filament is 0.3 to 0.5 of the entire penial length (less than 0.2 in *L. articulata*, Figures 65–67) and the glandular disc is usually about half the size and less swollen. No other anatomical differences have been discovered, so that morphological identification of juveniles and females must rely on features of the shell.

It is possible that the differences in egg capsule shape mentioned above may prove to be consistent. Capsules in this group have been illustrated three times. Reid (1986a) showed capsules of *L. articulata* s.s. from north Queensland with a circumferential flange (diameter 248–265 µm, ovum about 65 µm). Those illustrated by Mak (1995) from Hong Kong were of similar shape, but

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**Figures 42–55.** Shells of *Littoraria sinensis* and *Littoraria articulata*. 42–52, *L. sinensis*. 42, 43, Lectotype of *Littorina sinensis* (Philippi, 1847); China (MNHN). 44, Hoi Ha, Mirs Bay, Hong Kong (BMNH 20010124). 45, Tai Ping Bay, Qingdao, China (BMNH 20010125). 46, Tai Po, Hong Kong (BMNH 20010126). 47, Yoshino River estuary, Kanazawa, Tokushima City, Shikoku, Japan (BMNH 20010127). 48, Shianzin, Shaanxi, China (BMNH 20010128). 49, Hai Gang, Xiamen, China (BMNH 20010129). 50, Tan Shui, Taipei, Taiwan (BMNH 20010130). 51, Aberdeen, Hong Kong (BMNH 20010132). 52, Kahiri, Maebaru City, Kyushu, Japan (BMNH 20010134). 53–55, *L. articulata*. 53, Tai Po, Hong Kong (BMNH 20010135). 54, 55, Aberdeen, Hong Kong (BMNH 20010137).



**Table 2.** Summary of differences between *Littoraria sinensis* and *L. articulata*—shell characters apply to specimens from north-western Pacific Ocean only.

Character	<i>Littoraria sinensis</i>	<i>Littoraria articulata</i>
Shell shape	Relative spire height can be taller (to 2.05 whorls slightly more rounded)	Does not attain such tall spire (relative spire height to 1.89—whorls flatter)
Shell sculpture	Grooves up to half to one times rib width; small shells can be almost smooth	Grooves up to one quarter rib width; small shells can be almost smooth
Columella	Shorter and more concave, giving more oval aperture; narrower inner lip of aperture more sharply raised	Longer, straighter, giving ear-shaped aperture; inner lip of aperture less sharply raised
Shell color	Paler, often indistinctly clouded pattern; alignment of dashes less marked	Darker, distinct dashes, well aligned into axial stripes at suture and periphery
Penis	Penial filament 0.3–0.5 total length of penis	Penial filament less than 0.2 total length of penis
Distribution	China, Korea, Japan	Southern China to India and Australia

larger (diameter 300–340  $\mu\text{m}$ , ovum 69–71  $\mu\text{m}$ ). The capsule of *L. sinensis* from Amakusa, Kyushu, shown by Kojima (1958) was a simple lens shape without a peripheral flange (diameter 350  $\mu\text{m}$ , ovum about 70  $\mu\text{m}$ ). Mak (1995) showed that in three *Nodilittorina* species egg capsule diameter varied by 39 to 53% and suggested that shape and sculpture are more consistently diagnostic of species than size. It is possible that the capsules he illustrated as '*L. articulata*' were indeed of that species rather than the sympatric *L. sinensis*, despite their large size, so that shape might be relatively constant within this species across its geographical range, but this remains to be investigated. Caution is necessary, however, since capsules swell and the flange becomes less noticeable between spawning and hatching (Berry, 1986, in *L. strigata*; Ho, 1987). The capsules shown by Reid (1986a) and Kojima (1958) are very similar respectively to the early and late (24 hours after spawning) capsules of *L. strigata* (Berry, 1986: fig. 1) and might not represent genuine interspecific differences.

The characteristic features of the shells of *L. sinensis* and *L. articulata* are difficult to describe or quantify, owing to considerable intraspecific variation. Nevertheless, with experience sympatric samples can usually be successfully identified (as confirmed by penial shape of males) from their shells. The size range is similar (maximum 20.6 mm in *L. sinensis*, 19.0 mm in *L. articulata*) and both attain larger size in mangrove habitats than on rocky shores. Overall shape is also similar, but examples of *L. sinensis* can attain a slightly taller spire (relative spire height up to 2.05, cf. 1.89 in *L. articulata*) and the whorls are a little more rounded. In *L. articulata* the columellar pillar is longer and straighter, so that the ap-

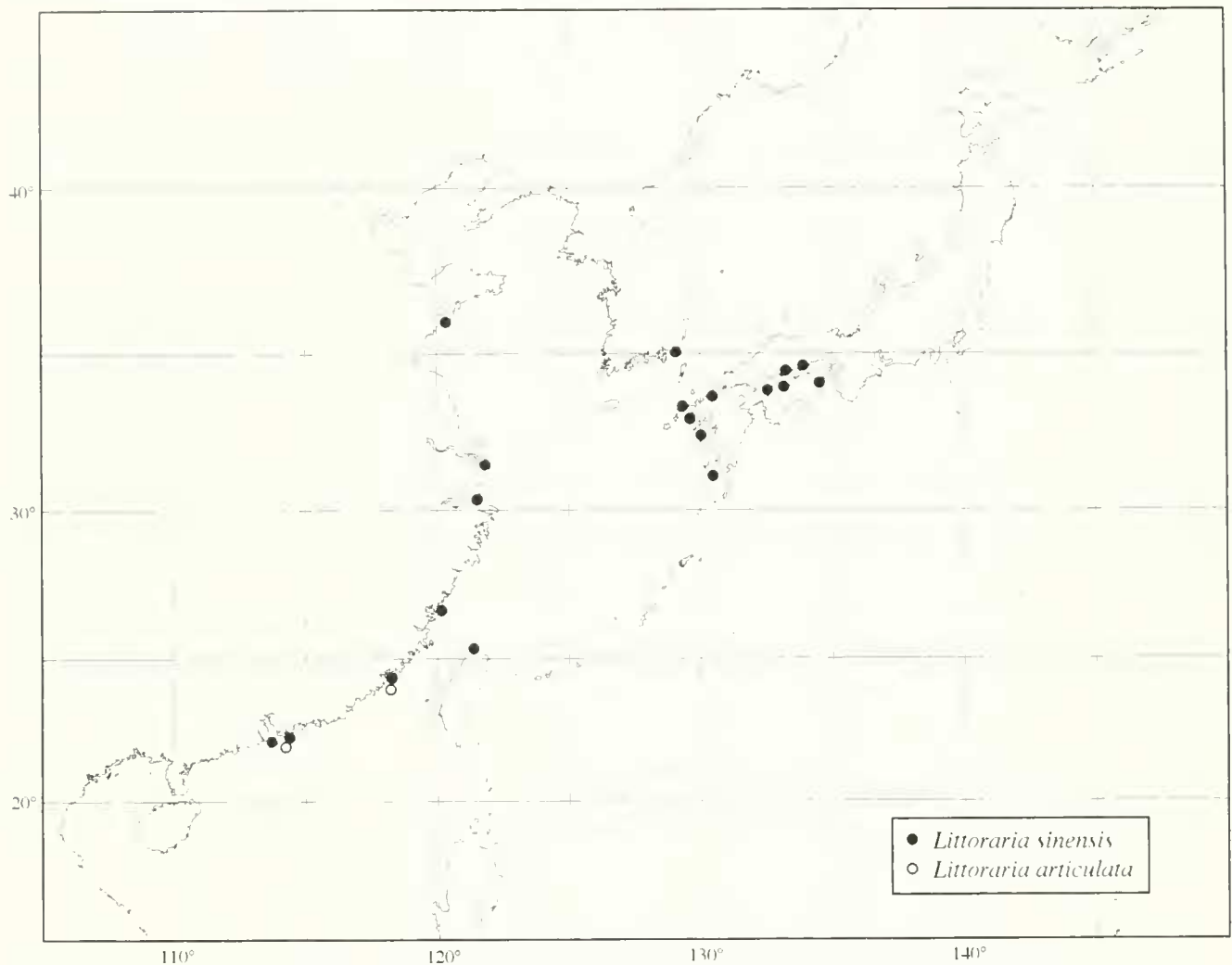
erture appears more ear-shaped. In contrast the columella of *L. sinensis* is slightly shorter and a little concave, and the aperture therefore more nearly oval. The columella of *L. sinensis* is usually narrower, but still deeply excavated, and the inner lip of the aperture (adjacent to the concavity of the columella) is more sharply raised, sometimes so much so that a slight umbilical crack is present. Both species share a similar count of primary grooves and of ribs on the body whorl, and both sometimes display dwarf forms with smooth shells in which grooves are present only as impressed lines. However, in larger and more strongly sculptured examples the grooves of *L. sinensis* are always more pronounced (up to half of, or even equal to, width of intervening ribs, compared with maximum of one quarter of rib width in *L. articulata*) and such shells are unmistakable (Figures 46, 47).

Shell color and pattern are likewise difficult to characterise, but often assist identification. *Littoraria sinensis* is usually paler, typically with a more finely mottled or tessellated or indistinct 'clouded' pattern, in which whitish flecks are present between the darker dashes. In both species the dashes are more or less aligned into oblique axial series, although this is usually only pronounced at the suture and periphery of each whorl, giving rise to short axial stripes at these points. This alignment is often more developed in *L. articulata*, in which, at the periphery, the axial stripes extend across four of the spiral ribs (Figures 53, 54); in *L. sinensis* this alignment more often covers only two or three peripheral ribs (Figures 50–51).

These contrasting shell characters are emphasized by the figures of sympatric samples of the two species (Fig-

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**Figures 56–67.** Penes of *Littoraria sinensis* and *Littoraria articulata*. **56–64.** *L. sinensis*. **56.** Tan Shui, Taipei, Taiwan (BMNH 20010130; shell H = 11.0 mm). **57, 58.** Shek O, Hong Kong (BMNH 20010133; shell H = 8.6 mm, 9.1 mm). **59.** Ha Cang, Xiamen, China (BMNH 20010129; shell H = 9.0 mm). **60.** Huan Dan, Qingdao, China (BMNH 20010134). **61.** Okayama Port, Kojima Bay, Japan (BMNH 20010135; shell H = 7.2 mm). **62–64.** Nagae River estuary, Otogo, Okayama City, Japan (BMNH 20010136; shell H = 13.5 mm, 13.0 mm, 14.0 mm). **65–67.** *L. articulata*. **65, 66.** Shek O, Hong Kong (BMNH 20010139; shell H = 5.7 mm, 10.2 mm). **67.** Aberdeen, Hong Kong (BMNH 20010137). Dotted line indicates extent of opaque glandular portion of penial glandular disc.



**Figure 68.** Geographical distribution of *Littoraria sinensis* with, for comparison, the records of *Littoraria articulata* from the same area (see text for lists of records).

ures 46 and 53; Figures 51, 54, 55). Nevertheless, shells of the two can sometimes appear virtually identical (e.g. Figures 44, 55) and only penial shape is reliably diagnostic. Geographical locality can also aid identification, since the distributions are known to overlap only between Hong Kong and Niamen (Figure 68). In Hong Kong the sites of recorded syntopy are Shek O, Tai Po, Three Fathoms Cove, Wu Kwai Sha and Aberdeen, and Hai Cang near Niamen (all BMNH). These sites range from mangroves to moderately exposed granite boulders and both species are common, so that there is no evidence for different habitat preferences.

*Littoraria sinensis* is also closely similar to *L. strigata*, distributed from the Philippines and southern Vietnam to Indonesia, Malaysia and India. The features of shell shape and coloration described above also distinguish *L. sinensis* from *L. strigata*; the latter often has a more strongly aligned pattern of oblique axial stripes, and sculpture is weaker than in *L. sinensis*. Most importantly, the penial filament of *L. strigata* is long, tapering and

vermiform, 0.6 to 0.7 of the total penial length (Reid, 1986a).

*Littoraria (Palustorina) articulata* (Philippi, 1846)  
(Figures 53–55, 65–68)

Synonymy as in Reid (1986a), excluding the entries now listed under *L. sinensis* above.

**Distribution:** Records listed in Reid (1986a) from China and Japan all either apply to *L. sinensis* or the identification is doubtful. The following new records (all BMNH) have all been verified by anatomical examination: China: Hai Cang, Niamen; Hong Kong (Tai Po; Aberdeen; Shek O, Three Fathoms Cove; Beigang Island); Hainan, Vietnam: Sung Sot Cave, Ha Long Bay; Do Son, near Haiphong, Cambodia: Koh Ponce, off Sihanoukville. The species is abundant at localities all around Singapore (St John's Island; Changi Point; Sentosa; East Coast Park; Sarimbun; all BMNH), whereas the similar



species *L. strigata* is rare (see below). Only a single preserved animal of the *L. articulata/strigata* group has been seen from the Indian subcontinent; this specimen, from Bombay, was a male of *L. strigata* (see below), so the occurrence of *L. articulata* in the region remains to be verified. A single shell has been seen from Bandar-e-Khamir, west of Bundar Abbas, Iran (BMNH), with a color pattern resembling *L. articulata*. This would represent a range extension of either *L. articulata* or *L. strigata*, but positive identification requires anatomical examination.

*Littoraria (Palustorina) strigata* (Philippi, 1846)

*Littoraria strigata*—Berry, 1986: 144–149, fig. 1 (egg capsule).

**Distribution:** Additional material from South East Asia supports the suggestion that this species predominates in localities with clearer water, whereas the similar *L. articulata* is present in more turbid and estuarine sites in the region. The occurrence of this species in the Arabian Sea has been confirmed by a single male specimen from Bombay. The species is uncommon in Singapore, where *L. articulata* is abundant. New records (all BMNH): Singapore; Sarimbun; St John's Island; Changi Point, Malaysia; Kudat, Sabah, Thailand; Krabi, India; Colaba, Bombay.

**Remarks:** Nine additional ethanol-preserved samples have been seen, supporting the earlier conclusion that this is indeed a species distinct from *L. articulata*. The only diagnostic morphological character remains the shape of the penis, in which the filament is 0.6 to 0.7 of the total length.

## ACKNOWLEDGMENTS

This work was stimulated by the conjunction of a number of events: the unexpected discovery of an undescribed *Littoraria* species in northern Australia by M. Stuckey in 1995 (Stuckey and Reid, in prep.), questions from H. Fukuda about the identification of the Japanese '*L. articulata*' and my own observation of assortative mating and differential zonation between 'forms' of '*L. intermedia*' in south India. In addition, there was a growing realisation that very small but consistent differences in penial form could be of taxonomic significance (Reid, in press, a). Since 1985 I have examined much additional material of *Littoraria*, both personally collected and kindly sent to the BMNH by colleagues. My grateful thanks to those who have provided specimens for this study: G. Feulner (Dubai), H. Fukuda (Okayama University), E. Glover (BMNH), D. Kadolsky (London), Y.-M. Mak (Hong Kong), A. Matsukuma (Kyushu University), G. Pendred (Portsmouth), M. Stuckey (University of Western Australia), J. D. Taylor (BMNH), V. Héros (MNHN) kindly sent a type on loan. I thank the Tropical Marine Mollusc Programme of Danida (Denmark) for the opportunity to carry out fieldwork in India.

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